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REPORT NO. 87-09-09K

COMBINED STIMULUS CONTROL OF PEAK FREQUENCY AND SOURCE LEVEL IN THE ECHOLOCATING DOLPHIN (*Tursiops truncatus*)

FINAL REPORT

March 1988

Prepared under Contract N66001-85-D-0021, Task 0055 for the
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by

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March 1988

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ABSTRACT

Research trainers demonstrated stimulus control over dolphin echolocation emission in past discrimination studies. Other research revealed control can also be exerted over emitted source levels during detection studies. Combined control over the peak frequency and the source level of the echolocation emission of the dolphin has recently been achieved to 85% performance levels. The dolphin is trained to emit clicks from a fixed position on a bite-plate/ tail-rest station to insure accuracy in click evaluation. Sessions are conducted in a predetermined random schedule of testing. A collecting hydrophone relays echolocation clicks to a microcomputer system which reinforces the animal when criterion is satisfied. Initial training consists of shifting the source level (or amplitude) of the echolocation clicks while solving a detection task. The separate discriminative stimuli of two underwater tones gain control over high and low amplitude levels of the emitted clicks. A third tone, with two distinct repetition rates, is used to train the control over peak frequency output. The separate behaviors are combined by superimposing the repetition rate of the peak frequency stimulus over the pure tone of the amplitude stimulus.

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I. INTRODUCTION

Naval Ocean Systems Center conducts over ninety percent of dolphin echolocation research studies in the United States. Scientists working in this field hold many hypotheses to explain how echolocation emissions are formed. Precise behavioral control of the dolphin must be executed to investigate these theories.

Past echolocation research (Schusterman and Kersting, 1978) attained a high level of control over the dolphin's echolocation emissions through strict adherence of the subject to the experimental design. The dolphin performed a detection study under stimulus control by utilizing an underwater tone to delineate trial time duration. The trial tone terminated for an incorrect response and changed to a "bridge" tone for a correct response.

This trial tone shaped and maintained correct stationing behavior. If the dolphin backed out of the underwater hoop station during the trial (moving out of the correct testing position), the trainer terminated the tone (ending the trial). This procedure gained stimulus control over the echolocation emissions of the dolphin. Scientists conducted recording sessions to investigate the existence of low amplitude clicks (inaudible to the human ear). These sessions verified that stimulus control was possible and had been attained over dolphin click emission.

Two Atlantic bottlenose dolphins (Tursiops truncatus) completed a study conducted by Mackay (1981) to determine dolphin

capabilities for frequency control. Operant conditioning, using automatic feeders activated by specific frequency ranges, successfully exhibited that dolphins could indeed control their frequency output in the lower range of whistles (5-16 kHz).

Recent research revealed behavioral control can also be obtained over the amplitude level of the dolphin echolocation pulses. Moore and Patterson (1984) trained a dolphin to perform a detection task while under operant control of its emitted source levels. Detection performance maintained at ninety percent levels, while average energy output for high and low amplitude clicks showed differences up to 23 dB.

Dolphins demonstrate limited control over the output of their echolocation clicks. The clicks are instantaneous in emission and termination. The amplitude is increased or decreased at will, with no absolute relationship to a target under scrutiny. But scientists believe that targets, to a large extent, dictate the click parameters. The physical characteristics of the click that the dolphin acknowledges, controls, and utilizes are unknown. It is suspected that dolphins are not capable of independent control of the frequency and amplitude of their clicks.

II. EXPERIMENTAL DESIGN

A. Test Subject

The test subject is an adult male Atlantic bottlenose dolphin (Tursiops truncatus) named Heptuna. The dolphin is 19 years old and weighed 211.8 Kg with a body length of 277.8 cm by

the end of the three year study. Over the course of the experiment, the dolphin gained 45 kg and grew 17.8 cm in body length. Heptuna maintained on 56-59 kcal metabolizable energy/kg body weight, which is the equivalent of 7.7 kg of Columbia river smelt daily.

B. Test Enclosure

The dolphin is housed in floating ocean pens located in Kaneohe Bay, Hawaii. The testing pen measures 6.1 m by 6.1 m and the adjoining holding pen is 9.1 m by 6.1 m. Located on the deck of the test pen is a small room which housed the electronic equipment used to measure the dolphin clicks.

C. Underwater Test Apparatus

The dolphin stationed at a fixed point facing the electronics room during inter-trial intervals. From this location, he is sent to a bite-plate/ tail-rest assembly located one meter below surface level and facing away from the trainer. This position is the station for trial measurements and click analysis.

The bite-plate consisted of polystyrene material designed to fit the dolphin mouth. The use of the bite-plate ensured accurate click evaluation by positioning the dolphin's nasal sac region directly in line with the collecting hydrophone.
A 60 cm by 106 cm metal screen, centered one meter below the water surface, separated the dolphin clicks from the collecting hydrophone during inter-trial intervals.

D. Computerized Test Apparatus

Stimuli and reinforcer tones originate from an Apple IIE computer system. Realistic SA-150 integrated stereo amplifiers regulate the University Sound UW-30 underwater loudspeakers. An interrupter device separates the tone into two distinct interruption rates used for the high and low frequency stimuli.

The collecting hydrophone is a Bruel and Kjaer model 8103 with a flat response out to a frequency of 160 kHz ($\pm$3dB). The clicks channel through an Ithaco 4210 variable electronic filter, set to pass a frequency band of 1-165 kHz, to eliminate background noise from the harbor's biological community.

A multi-channel peakhold filter (designed by Naval Ocean Systems Center) separates the relative energy output into eight overlapping frequency filter bins with centers between 30-135 kHz (15 kHz band widths). The computer simultaneously measures and analyzes the clicks. The results become immediately available to the trainer on a trial-by-trial basis.

E. Trial Description

A trial begins when the stationing dolphin receives a hand signal to move into position on the bite-plate/ tail-rest assembly. The trainer initiates the amplitude tone superimposed with the correct frequency interruption rate for 3-5 seconds while the dolphin settles into a straight, stationary position.

The metal screen lowers out of position between the dolphin and the hydrophone, signalling the dolphin to emit clicks. The

trial time is limited to three seconds. After an incorrect response, the stimulus tone terminates and the screen raises into position. When the dolphin emits clicks of correct frequency and amplitude, the computer-controlled reinforcer tone immediately sounds underwater. The dolphin reacts instantly, and leaves the bite-plate to surface for his fish reward. A fifty trial session averages 45 minutes in running time.

F. Subject Motivation

Dolphin motivation maintains at high levels with the use of strict behavioral control over the inter-trial intervals. Past dolphin research (Herman and Arbeit, 1973) demonstrates that control over the inter-trial interval improves learning without adverse effects on motivation. Deprivation is not employed, and the subject receives a full ration to maintain an animal of his age and length. The behavior is easily maintained during the most difficult stages with the use of "time outs". The program designs keep the task within grasp of the dolphin's capabilities. Criterion changes within the program progress the dolphin toward the desired behavior.

III. TRAINING PROCEDURES

A. Amplitude Training

The first step of amplitude training is the general concept of "shout" or "whisper", and the dolphin masters the task quickly. Once he learns to move his amplitude up and down in separate sessions, it requires less than sixty sessions, using blocks of high or low amplitude trials, before the dolphin

exhibits stimulus control in a random presentation of trials.

A program tracks the dolphin's click output in real-time and reinforces the first correct click to initially capture the behavior. A second program averages the amplitude for all clicks produced in a trial and compares the average to the criteria to shape the behavior.

B. Bimodal Frequency Output

Bimodal frequency output is immediately observed in high amplitude trials. Bimodal output is the simultaneous occurrence of high relative energy in frequency levels at opposite ends of the frequency range as shown in fig. 1. During trials of average (200 dB) amplitude, the frequency spectra of the dolphin's clicks is either broadband, low frequency or high frequency. But in trials with amplitude levels above 203 dB, the relative energy output elevates in both low and high frequency ranges (bimodal), with minor energy output in the median range. Bimodal output, although noted for the record, is disregarded at this stage of training. Amplitude output and its control are primary at this time.

C. Precise Amplitude Control

The behavior of amplitude control in the dolphin is already documented (Moore and Patterson, 1984). But the degree of amplitude control in the documented study is at the presentation of random 5 trial blocks. Each block consisted of a series of trials with the same criterion. The subject of this study is further trained to exhibit stimulus control in a random

presentation of high or low amplitude trials. A Gellerman series determined the order of trial presentation.

D. Target Detection

Early "baseline" training incorporates simple target detection sessions into amplitude training sessions. The detection sessions remain separate as a means to get click emission and stable performance. Following sessions impose an amplitude criterion onto the working dolphin that steadily increases in difficulty as performance improves in the amplitude task.

The detection task itself is not taxing to the dolphin. The target is always situated in the same location of six meters directly in front of the dolphin. So target detection and amplitude control sessions successfully combined into a single task after seven sessions (350 trials) of alternate blocks of detection or amplitude trials. The dolphin maintained performance above 90% for the combined amplitude and detection criteria when presented with both tasks in a random series.

E. Precise Stimulus Control for Amplitude and Detection

The dolphin's response to the stimuli is checked for precision before moving into the next stage of training: frequency control. During the amplitude stage of training, two separate underwater tones condition the dolphin's response, while the computer reinforces the desired amplitude output. The tones differ in both frequency and location, but the dolphin responds to the more blatant stimuli of location (and not the intended

stimuli of frequency). Before moving into frequency training, the tones are reversed in location and gradually moved together until a single speaker is in use. This action forces the controlling stimuli for up (or down) amplitude to be high (or low) tone frequency.

F. Early Frequency Control Training

Confusion occurred between the amplitude and the frequency tasks in early training. The stimuli source (underwater speaker), relocated to the rear of the dolphin (from its original location over the front of the subject), helped to differentiate the frequency task from the amplitude task in early training. Stimuli are gradually moved toward a final location near the front of the dolphin as the subject improved in the separate tasks. Work concentrated on the frequency task, eliminating the detection task from the sessions. Amplitude/detection sessions ran as "baseline" sessions every week and later once a month. The separate approach to the frequency task to help the dolphin's progress proved ineffective. The dolphin continued to shift its amplitude in response to frequency errors during training sessions.

G. Precise Frequency Control

The specificity of frequency training required a program change from an averaging to a real-time framework of click collection and evaluation. Programs developed with a myriad of stages. The original real-time program reinforced the dolphin on the first correct click, without considering the large number of

previous incorrect clicks.

This design worked for the generalized concept of amplitude training, because the subject must build up (or down) its amplitude to reach the correct level. Clicks prior to the reinforcer tone usually approach criterion, which instills the basic concept into the dolphin. Frequency training requires reinforcement of a consecutive number of correct clicks or the dolphin does not comprehend the task.

H. Simultaneous Control over Amplitude and Frequency

Control over the amplitude, simultaneously with frequency output, is necessary to eliminate confusion of the two closely related tasks. The dolphin typically uses clicks of 200 dB for detection work before any training in amplitude control. The equipment range centers at the dolphin's normal amplitude output. The subject learns to maintain amplitudes within 185-195 dB for low amplitude trials and 205-215 dB for high amplitude trials.

When faced with frequency criteria, the dolphin continued to shift its amplitude when the correct response is a change in frequency. High amplitude clicks (with inherent bimodal output) are of interest, so the chosen amplitude criteria to incorporate into the frequency trials is >195 dB. The high amplitude tone, with the repetition rate of the selected frequency stimuli superimposed over it, achieved both amplitude control and frequency control simultaneously. The amplitude variable is eliminated at this point and training centered on frequency control.

I. Bimodal Output Limited by Criterion Level

Frequency training in the high amplitude range requires a criterion design limiting the amount of bimodal output in the energy spectra of the emitted clicks. Programs work with the dolphin's output and gradually restrict it until the desired click parameters are met.

When the dolphin emits clicks above 204 dB, they are always bimodal in nature. The criterion is 60 kHz (or less) for low frequency and 105 kHz (or more) for high frequency. When the amplitude range of low frequency clicks reaches 203-210 dB, the energy spectra is bimodal. When the amplitude of high frequency clicks is 204-215 dB, the energy spectra is also bimodal. There are no exceptions to the case at these amplitude ranges.

It is interesting to note that low frequency clicks never reach amplitude levels above 210 dB. The four frequency filter bins in which the bimodal output occur are 45-60 kHz and 120-135 kHz. A criterion design to limit the amount of bimodal frequency output to 75% of the criterioh (or highest) bin value is successful in reducing bimodal output. This design checks the highest output in the opposing (incorrect) frequency range and allows it to be up to 75% of the total energy emitted in the highest bin of the correct range.

The relationship of the bimodal frequency output and high amplitude clicks is evident, yet not fully understood. The allowance of a certain percentage of bimodal output keeps the dolphin's motivation high in an otherwise difficult task.

Reinforcement magnitudes shape the response toward a non-bimodal frequency output.

J. Program Development for Frequency and Amplitude

A program that follows the dolphin's click output in real time effectively shapes the frequency spectra of the clicks. The additional problem of bimodal output forces another change in program design. The dolphin does not respond to the restrictive (bimodal allowance level = .75) criteria by eliminating his bimodal output. He simply reduces it to conform to the criteria imposed upon him (see Graph 1).

After many months of development, a program design specifically aimed at eliminating bimodal output gave promising results. As in the original program design, bimodal energy in the incorrect frequency range is allowed in levels up to 75% (bimodal output level = .75) of the highest correct frequency output. The criterion judges the relative distribution of energy filtered in the frequency bins. In the next stage of training, the bimodal allowance in the criterion tightens each time the dolphin reaches 80% performance standards. The criteria levels tested are .75, .62, .50, and .35 bimodal output allowance.

IV. RESULTS AND DISCUSSION

A. Relationship of Amplitude and Repetition Rate of Clicks

The dolphin oscillates the repetition rate and the amplitude of its clicks when confused about frequency errors. Before the start of frequency training, distinct differences appeared in the repetition rate of high versus low amplitude

clicks when the amplitude task was under operant control. These results reveal a link between amplitude and repetition rate of outgoing clicks.

The trials during the first amplitude experiment are limited to three seconds and the number of clicks emitted during that time frame is recorded. During trials of low amplitude, there are twice (2:1) as many clicks emitted than for high amplitude trials. Eight weeks later, target detection is incorporated into the task and a second set of data is collected. The combined task of target detection and amplitude control exhibits the same phenomenon (2 low amplitude clicks : 1 high amplitude click). It appears that the repetition rate of clicks is a variable closely related to amplitude.

B. Developing Control Over Bimodal Output

The emitted frequency spectra for target detection/ amplitude control is either broadband or low frequency with a peak at 60 kHz. So the first step in frequency training pursued high frequency control. When presented with this task, the dolphin appeared to add the high frequency output to his typical low frequency output. This posed the immediate problem of how to control the bimodal output through the criterion. Programs must further develop to shape the emitted response from bimodal to either high or low frequency.

The first set of frequency control sessions using a criteria check for bimodal output showed learning in seven 50 trial sessions. The program tracks the dolphin's emitted clicks with

an eight click rolling average, so the number of clicks required to reach criterion is an indicator of the dolphin's progress. When this figure stabilizes, the dolphin is at his peak performance for that criterion level.

The criteria of high frequency requires clicks at or above 105 kHz, and low frequency requires clicks at or below 60 kHz. The initial average click output to reach criterion at either level varies by 55 clicks for a single timed trial. After seven sessions, the average number of clicks required to reach criterion for either level varies by only 10 as shown in Fig. 2.

At this point, the dolphin is given progressively more difficult criteria concerning the amount of bimodal output allowed. As 80% performance levels are met, the criterion tightens to .62, .50, and finally .35 bimodal output allowance. This criterion allows the secondary energy peak at the opposing (incorrect) frequency level to be only 35% of the highest energy output at the correct level. The restrictions of the .35 bimodal output level caused an extreme response bias and the Einstellung phenomenon ensued (Schusterman and Kersting, 1978). The response bias acquired in the insolvable .35 criterion strongly influenced the attention of the dolphin in the solvable .50 criterion. During the following ten sessions at the .50 bimodal output allowance (a level where the dolphin is capable of 95% performance), performance remained at 70% levels due to this phenomenon displayed in Fig. 3. To remedy the situation, the subject is regressed to the easiest level of .75 bimodal output

allowance. As 80% performance standards are met, the dolphin is stepped through the following criteria (.62 and .50) in six sessions as shown in Fig. 4. The .35 bimodal output allowance is omitted as the final training criterion due to its apparent difficulty level.

C. Relationship of Amplitude and Bimodal Output of Clicks

The dolphin's response to errors in the restrictive bimodal output allowance (.62 and .50 criteria) was to change his amplitude. This developed into different amplitude levels for high versus low frequency output during training. The subject remained above 85% in performance levels at frequency control, but distinctly varied its amplitude output between high and low frequency trials.

This problem necessitated the early addition of amplitude to the criterion (before accomplishing complete frequency control). The variable of amplitude had to be stabilized before further restrictions on frequency criteria could be effective in training.

The final test program combines the high amplitude stimulus (pure tone) with the frequency stimulus (interruption rate). A criterion range of 20 dB for the emitted amplitude levels is added to prevent large deviations from criterion. The dolphin's performance, measured in amount of clicks required to reach criterion, stabilized after 200 trials.

Testing continued for an additional 550 trials to investigate the effect of learning. Curiously, there was no

learning effect. The dolphin continued to maintain an amplitude difference of 13 dB between high and low frequency output. After 750 trials, low frequency averaged 197 dB, while high frequency was 209 dB. But average clicks required to reach criteria varied by only 5 clicks between frequency criteria.

Results display approximately 20% of trials with reversed or atypical amplitude outputs. During these trials, the dolphin switched the amplitudes it usually associates with the separate frequency criteria. The average energy spectra for low frequency is a perfect sweep, with peak energy at 45 kHz. High frequency remains slightly bimodal, with peak energy at 135 kHz and a small secondary peak at 45 kHz. The dolphin continued to produce bimodal output, although its progress indicated task comprehension as displayed in Fig. 5.

The bimodal output of the individual trials is related to the amplitude emitted. During trials with amplitude levels above 203 dB, measured frequencies are always bimodal. This was initially thought to be confusion between the two tasks of frequency control and amplitude control. But after extensive testing of progressive software revisions, there appears to be a physical rather than psychological reason for bimodal frequency output in the echolocating dolphin.

D. Bimodal Output in Past Research

Previous research in echolocation beam pattern measurements (Au, 1978) reveal bimodal frequency output at the identical peak frequencies (60 kHz and 120 kHz) recorded in this

study. Simultaneous measurements taken at the melon and 1 meter ahead of the echolocating dolphin record high frequency (peak at 120 kHz) at the melon and bimodal (60 and 120 kHz) at the location 1 meter ahead. Additional measurements taken at the rostrum tip reveal signals that travel away from the major beam axis. This finding suggests that pulses reflect or refract from internal areas (possibly cranial bones).

E. Effect of Internal Click Reflection

A final stage of testing is set to investigate this internal interference effect on the dolphin's outgoing clicks under stimulus control. Neoprene of 1/8" thickness, layered on the top and bottom face of a identical bite-plate, prepares an alternative testing situation. Possible interference from the lower jaw bones is blocked by the reflective quality of the neoprene.

Random 30 trial sessions with either the polystyrene or the neoprene-covered polystyrene bite-plate are conducted for comparison. The same criteria of high (>105 kHz) and low (<60 kHz) frequency with amplitude level at >195 dB and amplitude range set to 20 dB tests the effect of blocking possible reflection of clicks from the lower jaw of the dolphin.

Eight sessions with random use of bite-plate types are completed. Results indicate an amplifying effect of the reflected low frequency clicks from the lower jaw area. With the neoprene-covered bite-plate, overall amplitude levels of both high and low frequency trials are similar with a difference of

only 5 dB (the previous session set with the polystyrene bite-plate has a 13 dB difference). High frequency clicks are slightly lower in amplitude and low frequency clicks are higher in amplitude, while both maintain excellent frequency spectra as displayed in Fig. 6. This data concludes the study by explaining the origin of bimodal output and exhibiting stable amplitude levels for both frequency criteria.

V. CONCLUSIONS

The training of frequency control is very specific in comparison to the training of an amplitude control task in the echolocating dolphin. The dolphin exhibits the ability to change the frequency levels of its clicks instantly (click-by-click), and even produce clicks of dual energy peaks in widely separated frequency levels (bimodal).

Dolphins are capable of controlling the frequency and amplitude of their echolocation clicks independent of the object parameters under investigation. This capability operates frequency and amplitude independently when the testing apparatus is designed to eliminate reflected clicks (even internally reflected) from the area of the collecting hydrophone.

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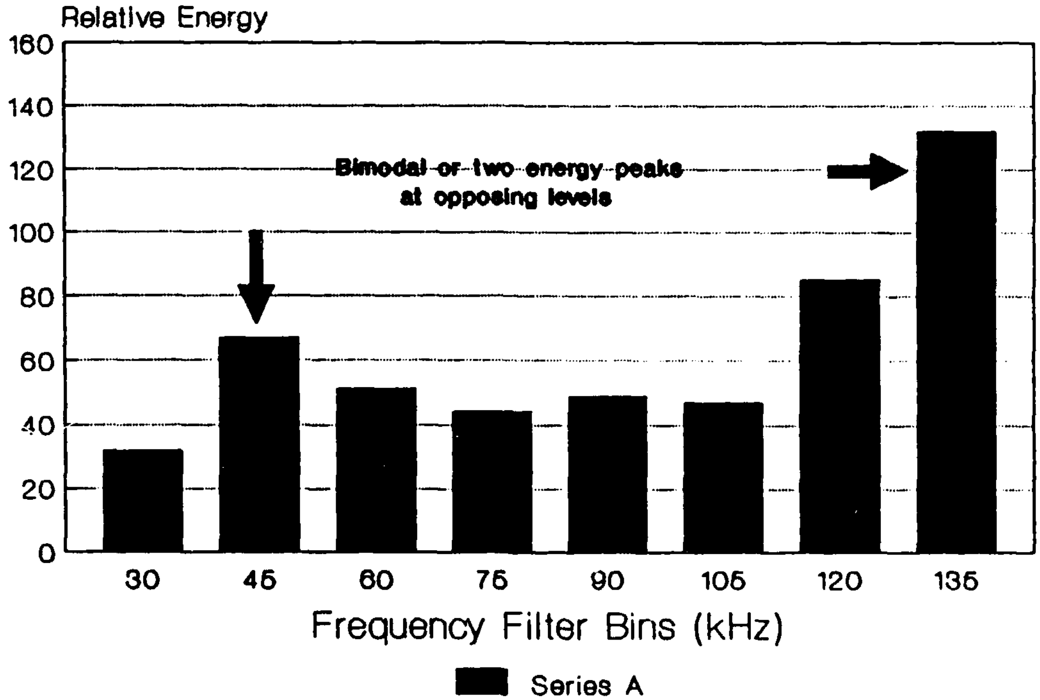
Example of Bimodal Output
High Frequency



During 95% performance levels

Figure 1.

TEST OF BIMODAL STOP PROGRAM
NO AMPLITUDE CRITERIA

CONTROLLED EMISSION DISCRIMINATION

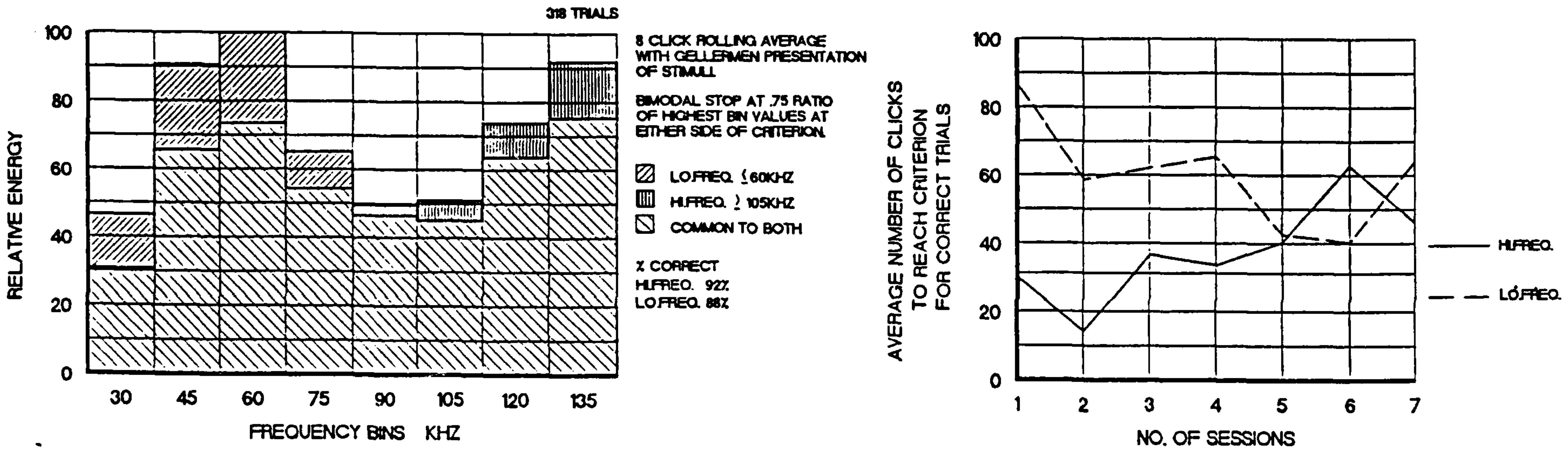


Figure 2.

TEST OF BIMODAL STOP PROGRAM

NO AMPLITUDE CRITERIA

CONTROLLED EMISSION DISCRIMINATION

CHANGES IN DIFFICULTY LEVELS

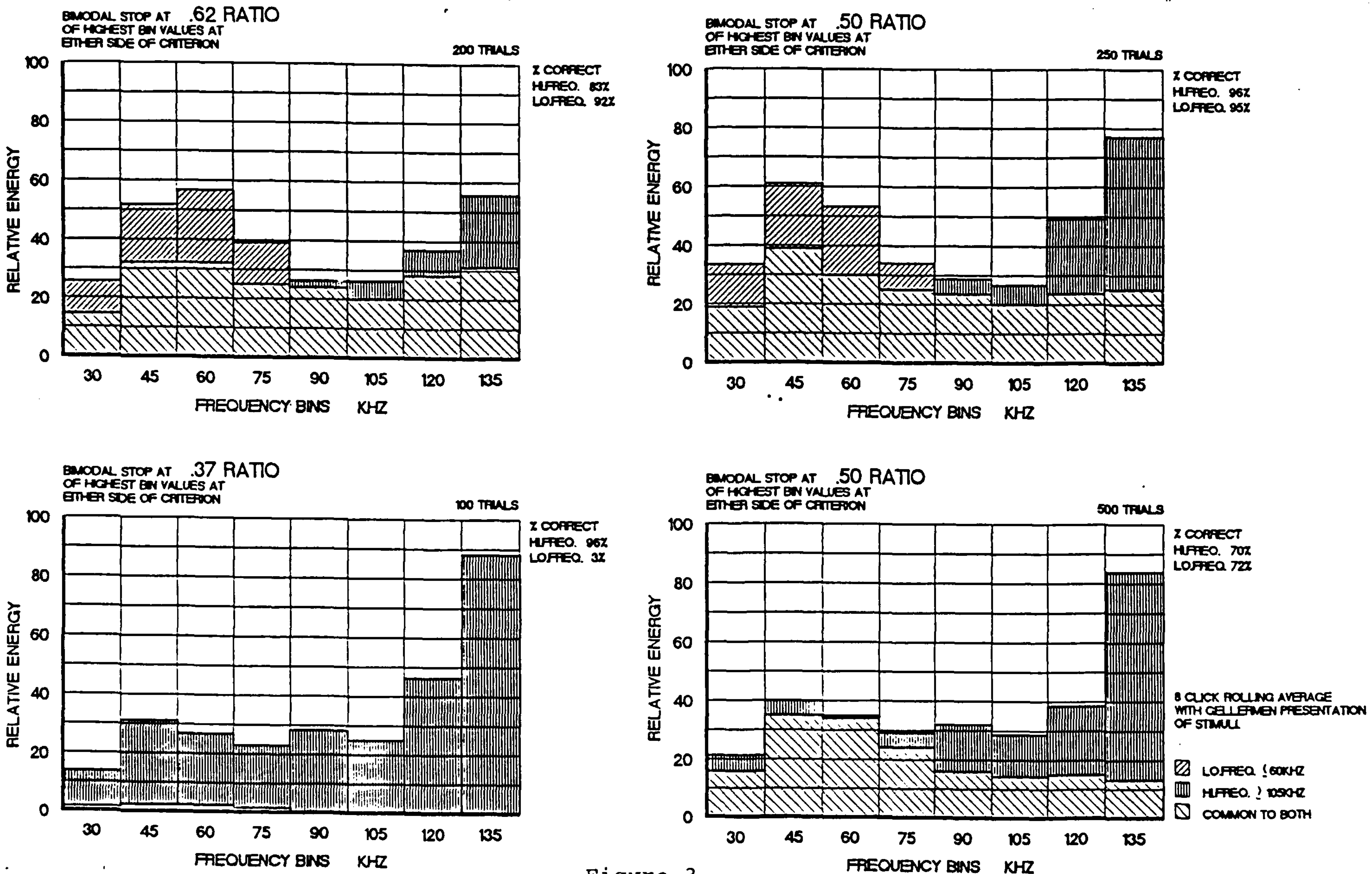


Figure 3

TEST OF BIMODAL STOP PROGRAM
NO AMPLITUDE CRITERIA

CONTROLLED EMISSION DISCRIMINATION

CHANGES IN DIFFICULTY LEVELS
RECOVERY PHASE

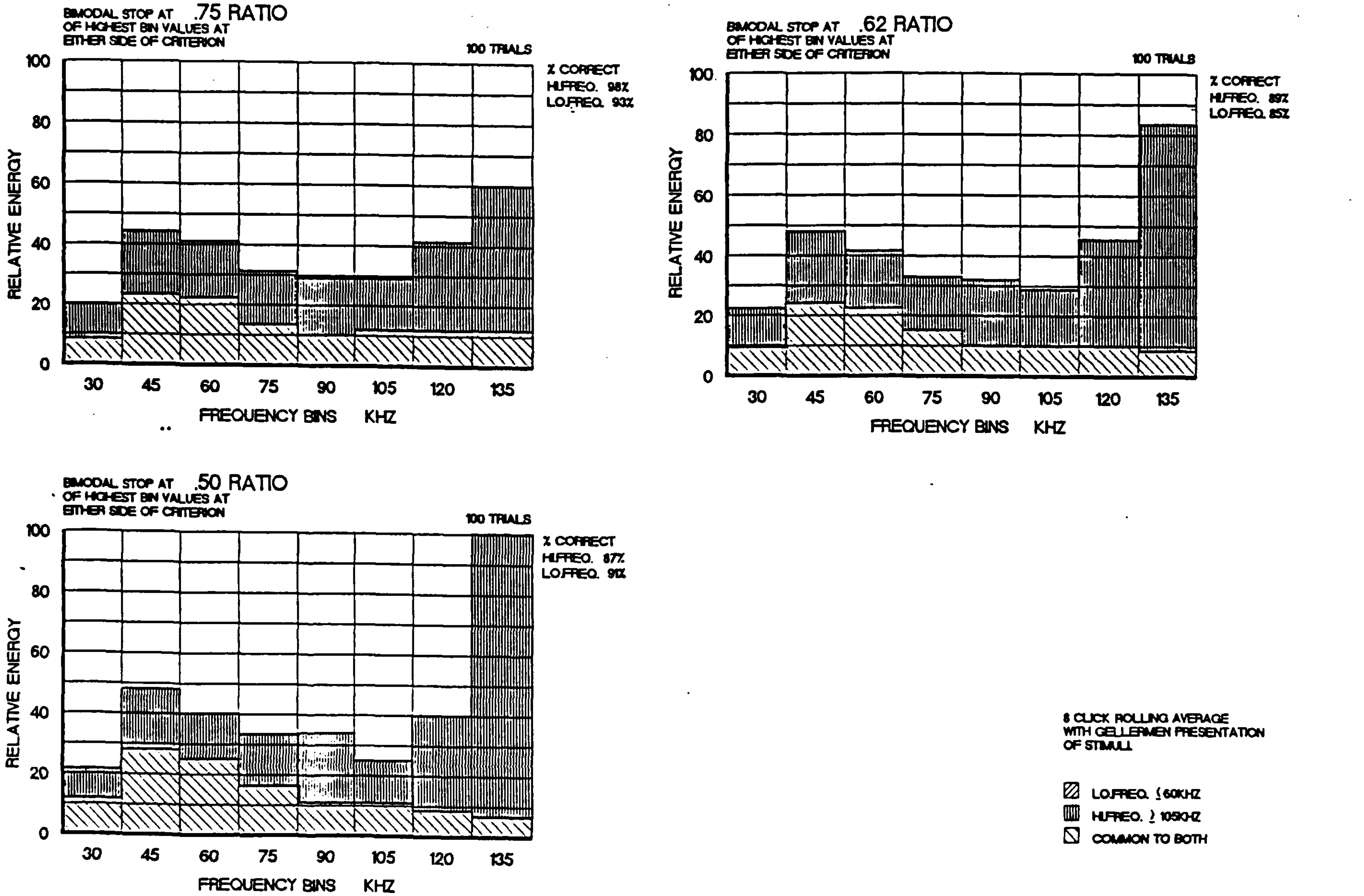


Figure 4.

TEST OF BIMODAL STOP PROGRAM
WITH AMPLITUDE CRITERIA

CONTROLLED EMISSION DISCRIMINATION

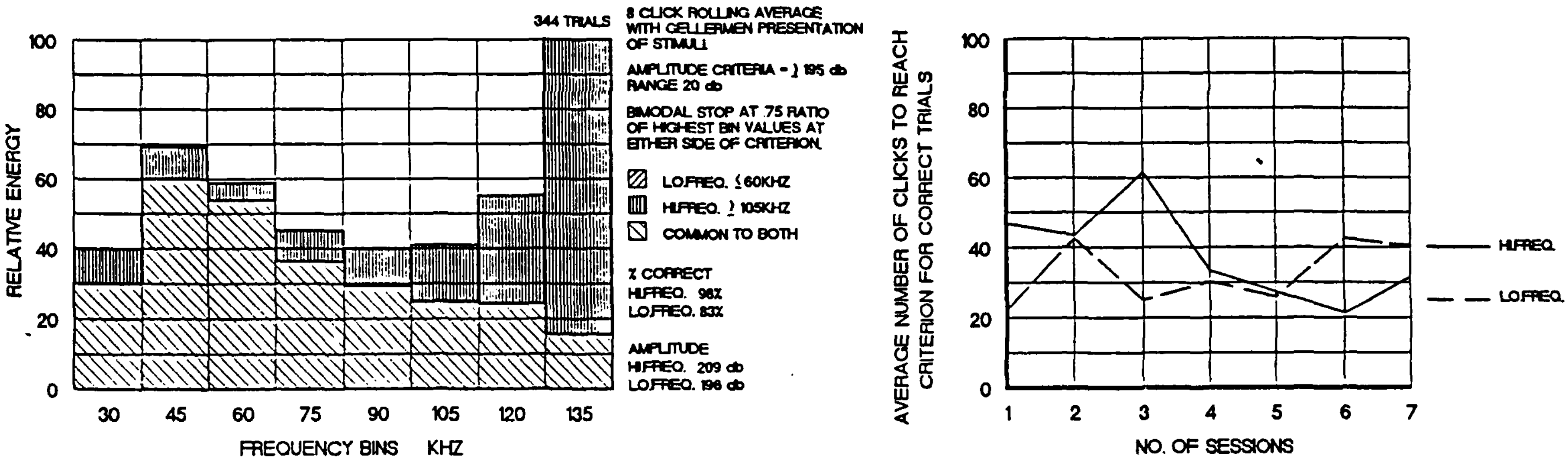


Figure 5.

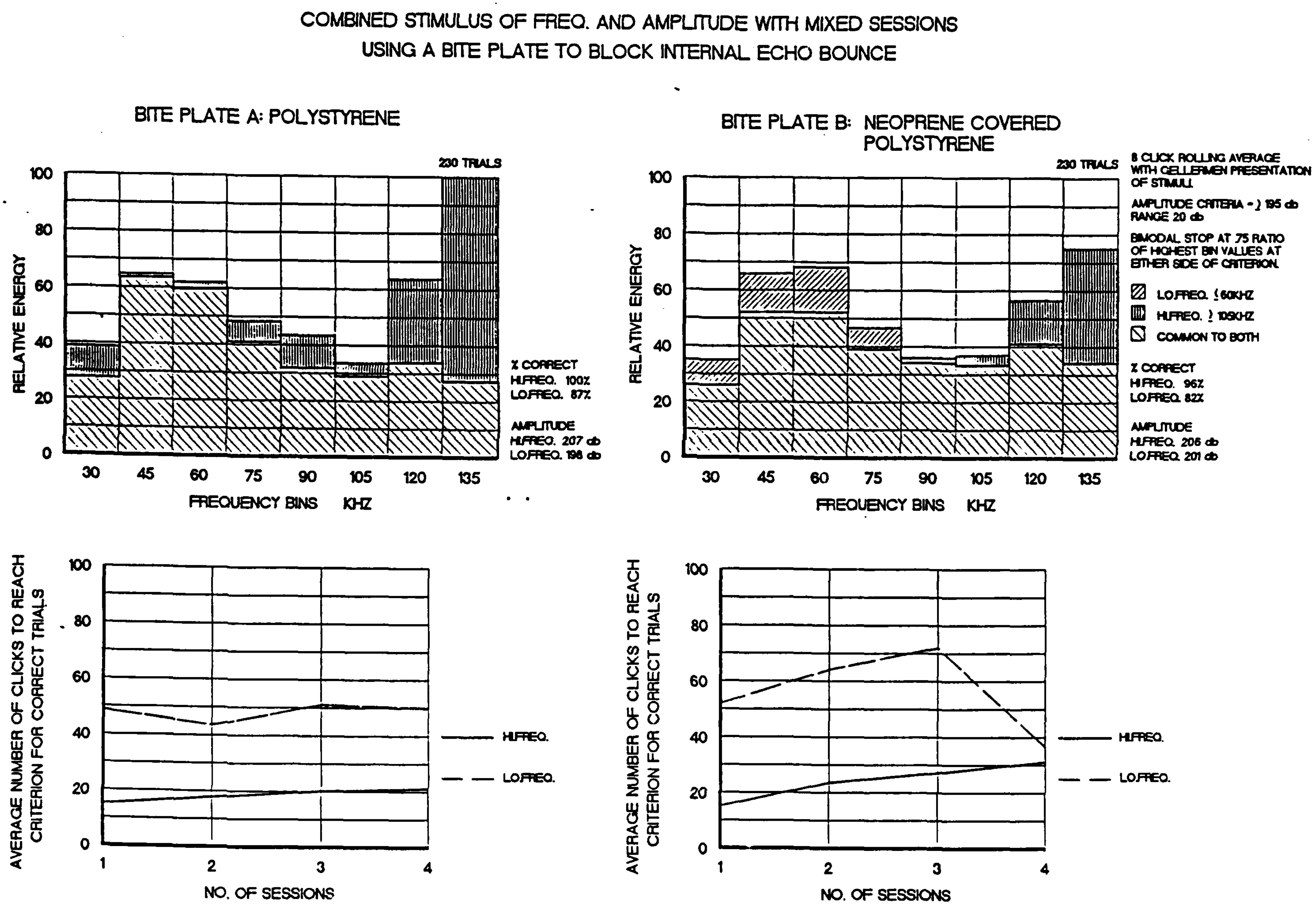

COMBINED STIMULUS OF FREQ. AND AMPLITUDE WITH MIXED SESSIONS
USING A BITE PLATE TO BLOCK INTERNAL ECHO BOUNCE
BITE PLATE A: POLYSTYRENE
230 TRIALS
RELATIVE ENERGY
FREQUENCY BINS KHZ
% CORRECT
HI.FREQ. 100%
LO.FREQ. 87%
AMPLITUDE
HI.FREQ. 207 db
LO.FREQ. 198 db
BITE PLATE B: NEOPRENE COVERED POLYSTYRENE
230 TRIALS
8 CLICK ROLLING AVERAGE WITH GELLERMEN PRESENTATION OF STIMULI.
AMPLITUDE CRITERIA - ≥ 195 db
RANGE 20 db
BIMODAL STOP AT .75 RATIO OF HIGHEST BIN VALUES AT EITHER SIDE OF CRITERION.
LO.FREQ. ≤ 60KHZ
HI.FREQ. ≥ 105KHZ
COMMON TO BOTH
% CORRECT
HI.FREQ. 96%
LO.FREQ. 82%
AMPLITUDE
HI.FREQ. 206 db
LO.FREQ. 201 db
AVERAGE NUMBER OF CLICKS TO REACH CRITERION FOR CORRECT TRIALS
NO. OF SESSIONS
HI.FREQ.
LO.FREQ.

Figure 6.